Title: Harbingers of change: towards a mechanistic understanding of anticipatory plasticity

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Abstract:

1. Phenotypic plasticity is a central avenue through which organisms cope with environmental heterogeneity by responding to cues of current environmental change to maximize fitness. If environmental change is impending and cues can reliably predict future conditions, organisms can also mount adaptive responses in anticipation of these changes if they possess the mechanistic architecture to do so (i.e., anticipatory plasticity).
2. Anticipatory plasticity has been documented across the tree of life, but how organisms detect and integrate cues of future conditions and mount anticipatory responses remains ambiguous. We synthesize theoretical principles from sensory biology and animal communication with recent advances in physiological ecology and extrapolate these insights to identify candidate mechanisms that may underpin anticipatory plasticity.
3. We discuss how ecological rhythms, cue detection and perception, and three major physiological mechanisms–the epigenome, neuroendocrine system, and the commensal gut microbiota–can contribute to the evolution and maintenance of anticipatory plasticity. We then integrate across these components by focusing on anticipatory plasticity in reproductive phenotypes (i.e., anticipatory reproduction).
4. We close by detailing a series of open questions related to both the proximate causes and evolutionary consequences of anticipatory plasticity. We hope to shed light on the potential mechanisms that facilitate anticipatory plasticity in the face of environmental variation, and how these mechanisms may influence how organisms and populations respond to anthropogenic change.

1 INTRODUCTION

"It is difficult to predict, especially the future." -Niels Bohr

Heterogeneous environments are widespread in nature, and compared to theoretically uniform environments, impose higher fitness costs for the organisms that inhabit them (Levins, 1968). In the absence of reliable information about shifting environmental conditions, organisms can minimize these costs by employing a number of different strategies to cope with unpredictable change (Dantzer, 2023). For instance, organisms can produce a single, canalized phenotype (Waddington, 2014): the remarkably consistent production of the complex *Drosophila* compound eye preserves the optimal development and function of this important trait despite environmental instability (Tsachaki & Sprecher, 2012). Bet-hedging is another strategy to deal with heterogeneity when reliable information is unavailable (Kvalnes et al., 2018; Simons, 2011). By producing a mix of phenotypes through random phenotypic variation, bet-hedging can maximize geometric mean fitness of the population over the long-term when fitness optima oscillate, ensuring that at least some phenotypes will match environmental demands (Tufto, 2015). This strategy may pre-adapt populations to the impending effects of human-induced rapid environmental change (HIREC), which are expected to be largely unpredictable (Crowley et al., 2016; van Baaren et al., 2024).

But when reliable information about environmental conditions is available, phenotypic plasticity–in which a single organism can produce multiple different phenotypes--is expected to evolve (Scheiner, 1993; West-Eberhard, 2003). Also termed “responsive plasticity”, phenotypic changes in response to cues of current environmental conditions are widespread in nature, occurring during development, within generations, and/or across generations (Snell-Rood, 2013; West-Eberhard, 2003). In response to changes in rainfall, birds can flexibly shift breeding behavior and timing (Nussey et al., 2005); in response to drought, plants can alter leaf morphology to reduce water loss (Gratani, 2014); in response to changes in photoperiodic shifts, insects can adjust rates of development and growth (De Block & Stoks, 2003). These responses, when adaptive, can facilitate population persistence even if they constrain genetic responses to selection by shielding genotypes from environmental variation and selection (Huey et al., 2003; Muñoz & Losos, 2018; Price et al., 2003).

In some cases, organisms can respond to predictive cues, or “harbingers”, of the future environment rather than the current one (i.e., “cued” or anticipatory plasticity, (Dantzer, 2023; West-Eberhard, 2003)). Anticipatory plasticity necessarily elongates the temporal lag between when organisms receive a cue and when the environmental conditions indexed by that cue will occur, and thus when fitness benefits can be reaped (Mariette, 2020). This lag can occur within an organism’s lifetime or span generations [e.g., anticipatory parental effects (Marshall & Uller, 2007)]. Although anticipatory plasticity has received comparatively less attention, environmental heterogeneity strongly favors its evolution (Jablonka et al., 1995; Lachmann & Jablonka, 1996), and anticipatory responses are expected to evolve under two conditions: first, cues of the future environment must be available and reliable (Bonamour et al., 2019; Levins, 1968; Reed et al., 2010; Scheiner, 1993). Unreliable cues can hamper the evolution of anticipatory responses, and the lag between predictive cue and future environment introduces considerable risk of error in both cue fidelity and perception (Gavrilets & Scheiner, 1993; Moran, 1992; Reed et al., 2010). Second, organisms must possess the sensory and physiological architecture necessary to sense and integrate harbingers (Kronholm, 2022). These predictive cues may be complex to integrate, particularly when transmitted through ecological features different from the conditions they predict (Levins, 1968).

As HIREC continues to rapidly reshape ecosystems, discerning how organisms will respond to future instability, and whether global change will alter the predictive architecture already in place in some populations, becomes paramount (Donelan et al., 2020). In this review, we synthesize what is presently known about anticipatory plasticity with recent advances in physiological ecology and sensory biology to begin building a mechanistic understanding of the causes and consequences of anticipatory plasticity. We discuss the evidence for anticipatory plasticity and the ecological context in which these responses may evolve, while outlining candidate physiological mechanisms that may govern cue integration and phenotypic coordination. Through this synthesis, we aim to shed light on the conditions in which environmental variability favors the evolution of anticipatory plasticity over other alternative strategies. We additionally aim to contribute to a mechanistic framework from which future studies can employ modern physiological and statistical tools to interrogate the bounds of anticipatory phenotypic plasticity in light of global change.

2 ECOLOGICAL RHYTHMS OF ANTICIPATION

Unlike random events with no intrinsic cyclicity, rhythmic environmental changes can generate a landscape of predictability for organisms in which future conditions are perpetually imminent and organisms are always some inevitable distance from that condition. Such rhythms may allow organisms to fine-tune their responses to predictive information, similar to Bayesian updating (Valone, 2006). The duration of these rhythms (short vs. long) and their regularity (regular vs. episodic) can vary as a function of environmental grain, which may favor different types of anticipatory plasticity. For instance, in predictable coarse-grained environments, anticipatory parental effects may offer an alternative to polymorphisms if parents can use predictive cues of the offspring environment to adjust offspring development (Bell & Hellmann, 2019; Burgess & Marshall, 2014; Lind et al., 2020; Marshall & Uller, 2007). Below, we discuss ecological rhythms common in studies of anticipatory plasticity.

2.1 Seasonal environments

Seasonal environments are defined by regular annual changes such as gradual changes in photoperiod, temperature, and precipitation. These shifts generate predictable annual fluctuations in vegetation growth, organismal behavior, and biodiversity. The cyclical and short-term nature of seasonal changes may make them more predictable than irregular or episodic changes, favoring the fine-tuned detection of both abiotic and biotic predictive cues of future conditions (Tolla & Stevenson, 2020). In seasonal environments, anticipatory plasticity often occurs in response to predictive cues of a hostile, dangerous, or nutritionally depleted future environment.

Organismal responses to seasonal change drive many of the phenological shifts common in seasonal environments, with many of those responses being anticipatory in nature (Réale et al., 2003). In a clear display of anticipatory behavioral plasticity, migratory birds flee to warmer regions as winter approaches (Kölzsch et al., 2015), and Atlantic salmon (*Salmo salar)* shift foraging behaviors ahead of seasonal changes in energetic demand (Bull et al., 1996). Many taxa, including insects and small mammals exhibit remarkable metabolic flexibility in response to seasonal cues of impending nutritional scarcity (Heldmaier et al., 2004). Insects slow development and metabolic activity during dormancy or diapause (Kostál, 2006), which has evolved multiple times across different taxa (Tauber & Tauber, 1981) and life history stages (Denlinger, 1986), suggesting broad adaptive value of this anticipatory response. In Arctic ground squirrels (*Urocitellus parryii)*, both the onset of hibernation occurs and the timing of emergence include a cascade of anticipatory metabolic changes ahead of a seasonal reduction in resources (Sheriff et al., 2012). Organisms can also enhance survival despite impending seasonal hostility through anticipatory morphological shifts in traits like coloration and reproductive structures. Arctic foxes (*Vulpes lagopus)* and snowshoe hares (*Lepus americanus)* undergo seasonal molting of their brown coats, growing white fur ahead of winter (Hersteinsson & Hersteinsson, 1989; Nagorsen, 1983) and enhancing predator escape (Merilaita & Lind, 2005). Many salmon undergo morphological changes to gonad size regulated by shifts in sex steroid production prior to swimming upstream to spawn (Truscott et al., 1986).

2.2 Resource pulse environments

Resource pulse events are infrequent, short-lived, and dramatic increases in a particular resource (Yang et al., 2008). Resource pulses are characterized by inherent temporal rhythms, occurring along a continuous scale. But unlike seasonal changes, these events occur episodically and intermittently rather than regularly over time (Yang et al., 2008). Distinguishing between environmental variability, seasonality, and resource pulses can be nebulous, but Yang et al. (2008) suggest a consumer-centric approach whereby pulses are defined by 1) their irregularity, brevity, and intensity *relative* to consumers, and 2) the extent to which they cause perturbations to consumer ecosystems (Yang et al., 2008). By this definition, many large-scale ecological events can be considered resource pulses, including the terrestrial productivity triggered by El Niño-Southern Oscillation rainfalls (Thomsen et al., 2018), coral reef spawning events (McCormick, 2003), and the 13- and 17-year emergence of periodical cicadas (Williams & Simon, 1995), each which ephemerally increase food availability for relevant consumers.

In terrestrial ecosystems, mast seeding is a common type of resource pulse in which plants (including trees like oak, maple, beech, and spruce) produce large quantities of seeds in some years but little to no seeds in others (Kelly & Sork, 2002; Nowlin et al., 2008). The evolutionary function of mast seeding may be a “swamp and starve” strategy in which trees overwhelm seed predators with more food than they can consume (Fletcher et al., 2010; Zwolak et al., 2022). It may also serve to increase pollinator efficiency (Moreira et al., 2014), or represent anticipatory plasticity by plants to increase reproduction in years when offspring survival is favored (Pearse et al., 2016). In contrast to unpredictable resource pulses like the El Niño-Southern Oscillation (Yang et al., 2008), mast seeding appears predictable to many consumer populations [e.g., (Boutin et al., 2006; Tissier et al., 2020; Vekhnik, 2019)]. While the precise mechanisms underlying consumer anticipation of upcoming mast events remain unknown, the predictability of mast seeding may favor the evolution of anticipatory plasticity as a counter-strategy by which organisms can optimally time phenotypic responses to maximize fitness in the face of extreme variability (Boutin et al., 2006).

Moreover, the strength of selection for anticipatory plasticity may hinge in part on the stability of the pulsed resource. Some pulsed resources are highly destructible, like the sudden aggregation and emergence of insects (Yang, 2004), while others can be collected and stored for future use, like seed (Marcello et al., 2008). The duration of resource availability during and after a pulse may thus modify the time lag between cue detection and the phenotypic response period. Stable resources that remain accessible or can be stored for future use may extend the phenotypic response period, allowing for lower precision and greater flexibility in the anticipatory response. By contrast, unstable resources that are available for only a short period of time may favor fine-tuning of anticipatory responses to increase precision (**Figure 1**). Thus, the strength of selection for anticipatory plasticity may increase linearly with the perishability of the resource, such that organisms aim to maximize their use of a time-sensitive resource pulse while simultaneously minimizing the likelihood of failure to detect the cue or respond incorrectly. This framework can be applied more generally to anticipated plasticity in response to changes in non-pulsed resources, for example, by considering how easily seasonally-fluctuating mates or individual territories can be monopolized.

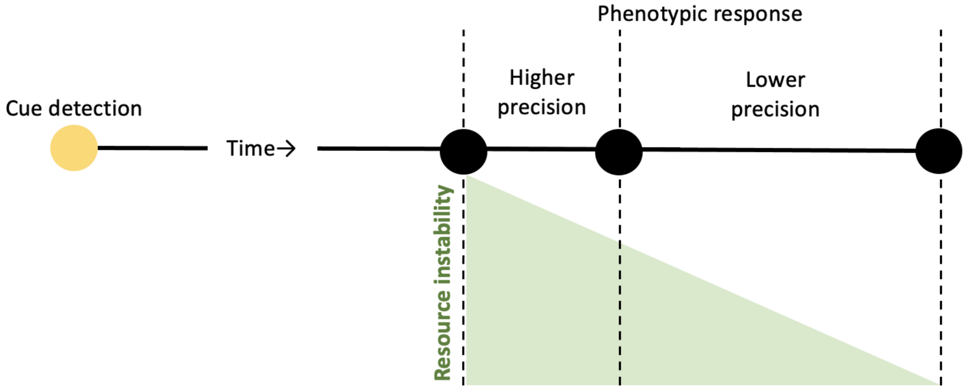


Figure 1. **Anticipatory plasticity as a function of pulsed resource stability.** Stable or easily monopilzed pulsed resources may extend the future selective period in which an anticipatory response is favored, relaxing selection for precise detection of predictive cues. Perishable resources may favor the evolution of highly precise anticipatory responses because they shorten the selective period in which fitness benefits of anticipatory plasticity can be reaped.

2.3 Social rhythms

Social environments are presumed to be largely unstable and unpredictable, but regular temporal and spatial fluctuations in social partners, mates, and competitors can occur, generating predictable shifts in the social environment that may favor the evolution of anticipatory plasticity. Changes in social composition can cue changes in future mating opportunities, resource accessibility, and reproductive risk. Populations of soapberry bugs (*Jadera haematoloma*) become male-biased due to seasonal increases in female mortality in anticipation of a future environment with high rates of male-male competition (Carroll & Salamon, 1995). In territorial North American red squirrels *(Tamiasciurus hudsonicus)*, females respond to anticipated increases in conspecific competition as a result of resource pulse events by accelerating juvenile postnatal growth (Dantzer et al., 2013). In insects, anticipation of resource-linked increases in density triggers anticipatory changes in sperm production, motility, and maturation that maximize male reproductive success when male-male competition is high (Gage, 1997). In some taxa, the dispersal of males into solitary life stages or extra-group coalitions leads to the inevitable introduction of novel males into established social groups, increasing infanticide risk (Lukas & Huchard, 2014). Such stratification of mating opportunities increases infanticide risk in other taxa may lead to the evolution of regulatory mechanisms of female reproductive investment in anticipation of likely offspring loss in the future (Roberts et al., 2012).

3 SIGNAL DETECTION THEORY AND PREDICTIVE CUES

Both responsive and anticipatory plasticity involve the transfer and receipt of information between sender and receiver, and can thus be conceptualized through the lens of animal communication.

Indeed, the terms “cues” and “signals” have been used interchangeably in studies of phenotypic plasticity, but are distinct phenomena. A cue describes ecological information that an organism uses to make a decision; cues can facilitate organismal “eavesdropping” on ecological information unintended for their perception (Bernal et al., 2007). By contrast, a signal is defined by its ability to elicit an intended response from the receiver, and has evolved through natural selection because of this intended response (Bradbury & Vehrencamp, 1998). Cues can evolve into signals when they gain precision through ritualization (Tinbergen, 1952), and signals can double as cues because optimized received detection can make signals more conspicuous to unintended targets (Roberts et al., 2007). Because we almost universally lack data on how evolution has shaped the ecological information that induces anticipatory plasticity, we will use the term cue to describe a feature of the environment through which an organism can infer future conditions.

Heterogeneous environments are inherently noisy because ecological information and the routes through which information transfer occurs can constantly change. Moreover, organisms can receive multiple cues indexing to multiple different environmental factors, and some of those cues can reflect current conditions while others reflect future conditions. Cue modalities can vary across taxa, life history stages, and ecologies because they require different sensory detection architecture. These complexities generate potential for unclear transfer of information, creating a “cocktail party problem” in which organisms need to discern relevant (e.g., related to fitness) cues from irrelevant background noise (McDermott, 2009). The temporal lag inherent to anticipatory plasticity may further increase the probability of cue infidelity and cue detection errors. Principles of signal detection theory can provide a framework for understanding the strategies that organisms inhabiting noisy environments can use to sense and respond to relevant cues while minimizing errors [(Getty, 1996)**, Box 1**].

Box 1. Signal Detection Theory (SDT) offers a framework for understanding how relevant information can be extracted and used by organisms in noisy environments (MacMillan, 2002). With its roots in electronic engineering and later adoption by the fields of psychology and neuroscience, SDT offers a powerful lens through which evolutionary biologists can interrogate how organisms communicate with their broader environments to anticipate future conditions. The associations between ecological cues and organismal responses are typically weak because of constraints related to both signal reliability (how well a cue indexes its condition) and receiver bias (how well organisms respond to those cues) (Getty, 1996)—these associations may be even weaker in anticipatory plasticity. In a given environment, an organism can thus respond to the presence (or absence) of information in 1 of 4 ways: (1) by correctly detecting a cue and responding to it (a “hit”), (2) by responding in the absence of a cue, or incorrectly detecting the cue (“false alarm”, (3) by failing to respond to a cue when present (a “miss”), or (4) by not responding in the absence of a cue (“correct rejection”) (**Figure 2A**). Wiley

(1994) applied this framework to animal communication to understand how organisms may balance the unequal fitness costs of false alarms and misses. Wiley hypothesized that organisms can minimize error costs by biasing their responses: when false alarms cost more than missed detections, under-responsiveness to cues prevents costly overconfidence; when misses cost more than false alarms, over-responsiveness to cues prevents costly missed detections (**Figure 2B**). Phenotypic responses that appear maladaptive, including no response at all, may instead reflect an adaptive balancing strategy to minimize fitness costs in heterogeneous environments. In attempting to discern the cues organisms use to elicit anticipatory responses, consideration should thus be given to seemingly non-adaptive responses that may obscure such broader strategies, particularly when deception (e.g., by a prey item) and some degree of general uncertainty (e.g., when ecological rhythms are episodic or irregular, such as in resource pulse ecosystems) are expected.

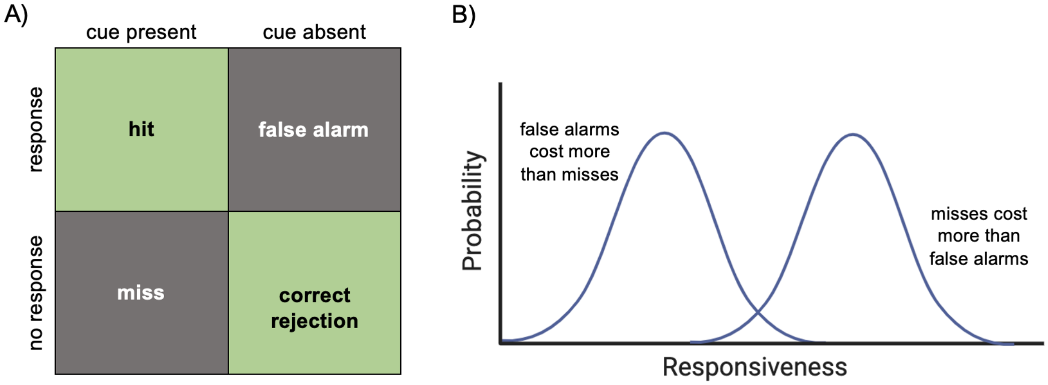


Figure 2. Organisms exhibiting anticipatory plasticity may bias cue detection to minimize errors and their associated costs. (A) In a heterogeneous environment with available cues of future conditions, organisms can phenotypically respond in one of four ways (green = phenotype-environment matches, gray = mismatches or errors). (B) The relative costs of different errors influence the degree to which organisms respond to cues, with higher rates of responsiveness when misses are more costly, and lower rates of responsiveness when false alarms are more costly (Wiley, 1994).

3.1 Cue fidelity

For anticipatory plasticity to evolve, cues must accurately foreshadow not only future environmental conditions, but the future selective environment, ensuring selection can act on the response (Moran, 1992; Reed et al., 2010). Unreliable cues increase mismatch between the optimal phenotype and environment (Ashander et al., 2016; Reed et al., 2010), influencing the likelihood of a transition between anticipatory plasticity and bet-hedging (Botero et al., 2015; Donelson et al., 2018; Tufto, 2015). Abiotic cues like photoperiod, temperature, and precipitation appear to be some of the most consistent predictive cues of impending environmental change (Bradshaw & Holzapfel, 2007; Whitman & Agrawal, 2009). Abiotic cues may offer enhanced reliability because they typically index seasonal changes, and are relatively stable compared to biotic cues that inherently hinge on the intrinsic traits and strategies of another organism. Indeed, social cues like vocalizations related to population density and the availability and quality of mates present greater opportunity for uncertainty and deception. Yet many anticipatory responses can be induced by biotic cues, alone or together with abiotic cues.

Because uncertainty is inevitable in changing environments, the fidelity of the predictive cues that organisms use to induce anticipatory plasticity may depend on the lag length between cue perception and the future environment. Indeed, this lag is thought to be a major constraint in the evolution of phenotypic plasticity writ large (DeWitt, 1998). Fidelity may decrease with an increase in lag (e.g., time between detection of a mast cue and the mast event itself; time between generations in species with elongated periods of gestation), because environmental stochasticity during this period can render otherwise reliable cues unreliable and increased mortality risk can leave the fitness benefits of an anticipatory response unrealized. Further, changes in the internal somatic state of an organism during this period (e.g., due to infection or injury), may impair or hinder an anticipatory response. As the lag length increases, cues may therefore grow more unreliable as selective pressures favoring the evolution of anticipatory plasticity in the system decline.

3.2 Cue modalities

Organisms can perceive predictive cues across multiple levels: at the highest level, information can be transduced across abiotic versus biotic pathways, as discussed above. Among biotic pathways, cues can be transferred across conspecific or heterospecific routes. Theory predicts that organisms will respond more robustly to information transmitted by conspecifics than by heterospecifics (Andersson, 1994), but organisms can respond similarly to both types of cues (Ord & Stamps, 2009). Indeed, conspecific cues appear to facilitate much of the organismal eavesdropping inherent to anticipatory plasticity, and in some cases, these conspecific cues can be central to the ecology and evolution of a species (Bernal et al., 2007). At the lowest level, cues can be transduced through distinct sensory modalities–we discuss some of the most common modalities identified in documented cases of anticipatory plasticity below.

3.2.1 Visual cues

Photoperiodic change is a common modality for predictive cues in seasonal environments. Increasing or decreasing day lengths can foreshadow widespread changes in both the biotic and/or abiotic environment associated with seasonality. Zooplankton use photoperiodic cues to induce diapause in anticipation of the future increase in predation risk associated with seasonal change (Slusarczyk, 1995). Biotic visual cues are common triggers for responsive plasticity as they can provide valuable information about current conditions, but they can also provide information about future conditions. The turrets of mud produced by cicada nymphs on the soil surface may alert mice to an upcoming emergence, facilitating adaptive shifts in foraging behavior and reproduction (Marcello et al., 2008). Visual exposure to specific food items during development can refine adult dietary preferences based on expected future food availability in cuttlefish [*Sepia officinalis,* (Darmaillacq et al., 2008)], and ground shadows of avian predators overhead can elicit movement responses in anticipation of falling prey in chickens (Wilson & Lindstrom, 2011). Changes in the appearance of buds and other reproductive structures may cue an upcoming resource pulse for consumers of masting species of trees (Boutin et al., 2006), while visual cues of fire may indicate an upcoming resource boom for consumers of fire-stimulated flowering plants (Beck et al., 2024).

3.2.2 Chemical cues

Both intra- and interspecific chemical cues can elicit anticipatory plasticity in the organisms that perceive them. In response to anticipated increases in sperm competition cued by social odors of rival conspecifics, bank voles (*Myodes glareolus*) developed larger seminal vesicles (Lemaître et al., 2011). Many anticipatory and cyclical behaviors, including those of spawning fishes, are regulated by conspecific cues, as well as chemical cues related to environmental quality (Buchinger et al., 2015). In palaemonid shrimps (*Palaemon argentinus*) chemical alarm cues produced by conspecifics induce anticipatory hatching and the production of larger larvae in (Ituarte et al., 2019). Kairomones, chemical cues in which only the eavesdropper benefits, can trigger anticipatory behaviors that facilitate predation or escape (Brown et al., 1970; Ruther et al., 2002). Organic compounds like amino acids found in mucus other excretions (e.g., urine) can serve as kairomones inducing phenotypic change. For instance, the development of anti-predator morphology is induced in *Daphnia* in response to predatory fish mucus (Brönmark & Hansson, 2012). Yet despite support for chemically-mediated anticipatory responses, precise identification of predictive chemical cues remains absent from many studies (Lutnesky & Adkins, 2003).

The synchronized seeding of masting trees may shed light on the cue modalities that seed consumers use to predict upcoming food booms in resource pulse ecosystems. Thought to be triggered largely by weather patterns like summer temperatures and precipitation, mast seeding is typically highly synchronous at local, but not continental, scales (LaMontagne et al., 2020; Pearse et al., 2016). Trees in close proximity may synchronize reproduction by responding to the same localized weather cues (Rees et al., 2002), but the underlying physiological mechanisms mediating masting remain ambiguous. One mechanism may be related to volatile organic compounds [VOCs, (Hagiwara & Shiojiri, 2020; Kon et al., 2005; Pearse et al., 2016)]. VOCs are a central pathway of conspecific communication in plants (Holopainen, 2004), and can serve as both cues and signals of impending conditions (Ninkovic et al., 2021). For example, plants can use conspecific VOCs produced in response to predation to prime defense systems in anticipation of future predation attempts (Morrell & Kessler, 2014). VOCs may also transmit information related to future resource abundance to heterospecifics. Although eavesdropping has been traditionally associated with visual and acoustic cues [e.g., predators eavesdropping on the mating calls of their prey, (Lehmann & Heller, 1998)], chemical cues can facilitate heterospecific eavesdropping that appears central to some species ecology and evolution (Bernal & Page, 2023).

3.2.3 Acoustic cues

Abiotic acoustic cues related to the movement of things like water, wind, and ice can foreshadow upcoming seasonal change, and biotic cues like conspecific vocalizations can foreshadow the future social environment (Rosenthal & Ryan, 2000). In multiple species of field crickets, juveniles adaptively adjust maturation rates in response to mating calls in the rearing environment that index the density and quality of reproductive competitors and mates in the future adult environment (DiRienzo et al., 2012; Kasumovic et al., 2011). Territorial vocalizations can serve a defense purpose and can reinforce territorial boundaries while also serving as cues of both current and future population density (Siracusa et al., 2017). In field crickets (*Teleogryllus oceanicus*), juvenile males reared in an environment abundant in the long-range calls of other males invested more in reproductive tissues and attained better adult condition compared to males reared in acoustically silent environments (Bailey et al., 2010).

3.3 Catalyst cues

The Pareto principle or “80-20 rule” may be observed in situations of anticipatory plasticity whereupon 80% of the response of a population to an ecological cue reflecting future environmental conditions are instigated, or catalyzed, by 20% of the individuals in that population using “catalyst cues”. This is analogous to leadership or keystone individuals in animal societies where an individual (“leader”) has power over other individuals, such as their daily activities [movement and time budgets: (Marshall et al., 2012; Owen-Smith et al., 2010)]. In this situation, a small number of individuals (~20%) may wield tremendous influence on where and how the other 80% of individuals spend their time. It is conceivable that the same principles may operate in cases of anticipatory plasticity, where plasticity exhibited by a small number of individuals (leaders) elicits the same plastic response in other individuals (followers). This could be labeled a form of “social power”, such as where an individual or group of individuals has coveted access to reliable cues of the future environment, exhibits adaptive plasticity to those cues, and others follow. Those cues the catalyzing individual or keystone individual gives to others could be inadvertent, like sensory cues emitted by reproducing individuals.

3.4 Co-opted cues

Cues that induce anticipatory plasticity may be transmitted through modalities directly related to the ecological factors they reflect, but they do not have be (Levins, 1968). Indeed, heterogeneous environments can generate substantial environmental covariance across multiple distinct environmental factors which may result in cue co-opting, whereby a cue related to one ecological feature provides predictive information about an entirely different feature. For instance, in eastern chipmunks, the abundance of one food item (red maple) serves as a cue of future abundance of another more fitness-relevant food item [beech seed, (Tissier et al., 2020)]. The use of co-opted cues may offer greater flexibility for receivers especially if they are composed of multiple different cue modalities, for example, by allowing an organism to detect one only component of the cue during a particular life history stage but a different component of the cue in a different stage. Moreover, because seasonality generates high rates of environmental covariance whereby many ecological factors change at once, co-opted cues may be more likely in seasonal environments.

3.5 Multimodal and mosaic cues

Environmental information can be composed of multiple distinct sensory parts (i.e., a multimodal cue) further transduced across multiple distinct modalities, resulting in a mosaic cue whose fidelity hinges on the sum of its parts. When detectable, mosaic cues can boost organismal fitness by fine-tuning processes of cue detection and response, particularly in highly variable environments (Dore et al., 2018). For example, *Drosophila spp.* use redundant auditory, olfactory, and tactile cues of fluctuating intraspecific competition to adaptively adjust reproductive behavior (Bretman et al., 2011; Maguire et al., 2015). Larval cane toads rely on a combination of abiotic (light levels) and biotic (chemical cues of conspecifics) cues to stimulate aggregation (Raven et al., 2017), and scatter hoarding rodents like chipmunks, gray squirrels, and deer mice use a combination of olfactory cues, visual cues, and memory cues to locate previously buried food items (Ramirez & Steury, 2024; Wall, 2000).

Complex cues can provide highly detailed information about environmental conditions and may boost the fidelity of predictive cues, particularly when the temporal lag between cue detection and the future environment is long. If one sensory modality is altered but the others stay the same, organisms may still be able to mechanistically decipher relevant information. Carnivorous bats can circumvent hampering of acoustic cues by noise when hunting by shifting to using visual cues to locate prey (Gomes et al., 2016). Cue shifting can also occur within the same sensory modality, like when fiddler crabs (*Uca vomeris)* switch from visual cues of predator speed to visual cues of predator retinal size during predation attempts (Hemmi & Pfeil, 2010). Multimodal and mosaic cues may offer organisms “escape routes” by adding complexity to cues and modifying the magnitude of risk associated with the time lag between cue detection and future conditions; however, these cues may be more susceptible to disruption if each component is necessary to transmit relevant information.

4 PHYSIOLOGICAL COORDINATORS OF ANTICIPATORY PLASTICITY

The high level of flexibility inherent to anticipatory plasticity may necessitate coordination by similarly flexible physiological machinery. Here, we discuss three distinct but related physiological mechanisms that may contribute to the mechanistic architecture underpinning anticipatory plasticity because they rapidly respond to environmental input and contribute to many of the phenotypes common in documented cases of anticipatory plasticity (e.g., behavior, reproduction, metabolism/growth) through multiple mechanistic pathways.

4.1 The epigenome

Alterations to chromosomal regions via chemical modifications of histones, DNA, and RNA (hereafter, epigenetic change) represent a promising mechanism by which organisms can coordinate anticipatory plasticity. Epigenetic alterations offer significant flexibility because they can shift patterns of gene expression without changes to the underlying sequence of amino acids and/or nucleotides [i.e., no change to the underlying genome, (Turner, 2009)]. Environmental fluctuations, including abiotic shifts in factors like ambient temperature and biotic changes in resource availability, induce epigenetic change in organisms with downstream effects on phenotypic expression (Jaenisch & Bird, 2003). Many of these fluctuations are the same as those that induce anticipatory plasticity, suggesting that the epigenome may be a major mechanism linking predictive cues of future environmental change to anticipatory responses. Epigenetic mechanisms of anticipatory plasticity can evolve in spite of variation in genetic architecture, particularly when cue fidelity is high (Kronholm, 2022).

Epigenetic effects may be central to anticipatory parental effects, acting as a principal driver of parental adjustments of offspring phenotype in response to cues of future conditions (Guerrero-Bosagna et al., 2018; Kronholm, 2022). For example, in fruit flies (*Drosophila melanogaster)* and nematodes (*Caenorhabditis elegans*), small RNAs are produced in response to nutritional stress. These small RNAs are inherited by offspring and subsequently alter offspring genetic expression to facilitate environmental matching (Duempelmann et al., 2020; Rechavi et al., 2014). Small RNAs present in seminar fluid may elicit anticipatory responses in females (Curley et al., 2011; Mashoodh et al., 2023), and can be transmitted across generations, suggesting epigenetic mediation of anticipatory parental effects even in the absence of parental care (Eaton et al., 2015). Epigenetic inheritance thus opens the door for environmentally induced change in parents to alter developmental trajectories of offspring in an anticipatory manner (Wang et al., 2017), facilitating an epigenetic-environmental matching across generations (Marshall & Uller, 2007).

As a role for epigenetic inheritance in anticipatory parental effects gains support, comparatively fewer studies have investigated potential epigenetic contributions to within-generation anticipatory responses. Yet many of the anticipatory phenotypic changes common in seasonal environments (e.g., migration, hibernation) are strongly encoded by circannual rhythms (Helm & Lincoln, 2017). These circannual rhythms are regulated primarily by the epigenome, and many of the underlying candidate gene pathways driving seasonal phenotypes are governed by DNA methylation (Alvarado et al., 2014). As the most “proximate” type of epigenetic change, DNA methylation may be central to within-generation anticipatory plasticity. Indeed, shifts in DNA methylation patterns accompany anticipatory physiological responses following exposure to glucocorticoid hormones in experimental rodent studies (Thomassin et al., 2001). Eastern chipmunks (*Tamias striatus)* adaptively increase reproductive output ahead of a pulse in beech seed production (Tissier et al., 2020) and they also exhibit concomitant increases in DNA methylation (Leung et al., 2020). In non-resource pulse years, however, rates of DNA methylation are low, and reproduction is minimal or absent entirely, suggesting that epigenetic variation may support anticipatory reproductive plasticity in this population (Leung et al., 2020).

4.2 The neuroendocrine system

In vertebrates, the neuroendocrine system is an integrator network that can sense cues of environmental conditions and coordinate downstream phenotypic responses (Dantzer, 2023; Martin et al., 2011). Complex physiological linkages between the nervous system (i.e., the brain) and the endocrine system (i.e., various organs and glands) serve to integrate intrinsic and extrinsic cues, resulting in both transient and long-term shifts in phenotype. The neuroendocrine system mediates many physiological processes central to organismal survival and fitness, including reproduction, growth, development, behavior, and the stress response, as well as governing linkages among these phenotypes.

The hypothalamic-pituitary-adrenal (HPA) axis, a cascade of hormonal feedbacks that begins with integration of environmental information by the brain and culminates in the production of glucocorticoid hormones (GCs) by the adrenal glands, is central to the physiological stress response and regulation of metabolism (Sapolsky et al., 2000). Anticipatory increases in GCs can be induced in response to a variety of cues, including those of conspecific rivals or predators (Boonstra, 2013), or merely in anticipation of the metabolic demands associated with either reproduction (in seasonally breeding animals) or migration (Romero, 2002). The HPA axis has thus been viewed as a primary mechanism mediating many anticipatory responses, particularly those that involve integration of predictive cues of environmental stress like anticipatory parental effects (Hau et al., 2016). Such effects may occur via direct transfer of GCs to offspring, or indirectly by altering parental care behavior (Champagne & Meaney, 2006; Moore & Power, 1986; Wilcoxon & Redei, 2007). For instance, anticipatory maternal adjustments to offspring growth in response to increased conspecific competition are triggered by maternal GCs in red squirrels (Dantzer et al., 2013). Similar parental effects have been uncovered in sticklebacks (Giesing et al., 2011) and mice (Santarelli et al., 2014), whereby mothers facilitate offspring phenotype-environment matching through altered GC production and/or transfer. In European starlings (*Sturnus vulgaris*), higher concentrations of yolk GCs enhance flight performance in fledglings (Chin et al., 2009). Other studies have documented concomitant, rather than causal, changes in GCs with anticipatory responses suggestive of HPA axis involvement. For instance, repeated predation attempts result in lower GC production and smaller clutches in female birds (Travers et al., 2010). GCs and associated enzymes (e.g., 11β-HSD I and II) are central to anticipatory physiological shifts in migrating birds, particularly before long migrations, in response to photoperiodic cues of impending seasonal change (Pradhan et al., 2019).

The preparatory changes associated with migration are also mediated by the hypothalamic-pituitary-gonadal (HPG) axis, which includes the release of many of sex steroids like estrogens, progesterone, testosterone (Ramenofsky et al., 2012). Prior to migration, changes in the HPG axis can enhance future flight performance by causing reproductive organs to shrink (Bauchinger et al., 2007); the preparatory release of androgens stimulated by photoperiodic cues can also increase fat stores that serve as the main fuel source for migration (Tonra et al., 2011). Anticipatory increases in testosterone production may enhance organismal performance in future competitive encounters (Gleason et al., 2009). Integration of both abiotic (photoperiodic) and biotic (demographic) cues by the HPG axis underlie sexual plasticity in fish (Liu et al., 2017), which can have implications for anticipatory responses to predicted composition of the social environment (Le Roy et al., 2017). Finally, the HPG axis offers a potential route through which plant secondary metabolites may influence reproductive physiology. Phytohormonal compounds like phytoestrogens found in plants can bind to estrogen receptors in vertebrate consumers of those plants, potentially altering reproductive physiology (Fidler et al., 2008; Labov, 1977).

Other hormonal cascades beyond the HPA and HPG axes may also play an important role in anticipatory plasticity. For instance, melatonin is released by the pineal gland and is critical for the maintenance of circadian rhythms, which are inherently anticipatory in nature, and which can mediate reproductive behavior (Ohta & Konishi, 1992). Ghrelin and leptin–hormones related to metabolism, appetite, and fat storage–may be key to anticipatory adjustments in metabolic phenotype ahead of changes in resource availability. Indeed, administration of leptin, which stimulates appetite, can modify brood numbers by acting as a cue of energetic supply in great tits [*Parus major,* (Lõhmus &

Björklund, 2009)]; ghrelin, which stimulates appetite, regulates preparatory feeding behavior in hibernators like ground squirrels [*Spermophilus lateralis,* (Healy et al., 2010)]. In some species, oxytocin and vasopressin are crucial to the integration of olfactory cues and may therefore be involved in the integration of predictive cues related to conspecific densities and predator abundance (Bielsky & Young, 2004).

4.3 The commensal gut microbiota

The past few decades have ushered in a growing appreciation for a regulatory role for the trillions of commensal and symbiotic microorganisms like bacteria that inhabit different host body sites in the broader physiology, behavior, and fitness of their hosts. Microbial symbionts, particularly those in the gastrointestinal tract where the microbiota is especially dense and diverse (hereafter, gut microbiota), are highly sensitive to both intrinsic (i.e., within-host) and extrinsic (i.e., environmental) inputs. As such, gut microbiota may be powerful transducers of predictive cues, and microbial sensing may expand the range of cues that a host can detect [e.g., by integrating non-photic cues to adjust host circadian rhythms, (Choi et al., 2021)]. Because microbiota have co-evolved alongside their hosts over evolutionary time (Lim & Bordenstein, 2020), they may ultimately serve as a mechanism of rapid ecological adaptation by providing the mechanistic architecture necessary to facilitate the evolution of anticipatory plasticity (Alberdi et al., 2016).

Gut microbiota can contribute to host responsive plasticity, for example by reorganizing in response to immediate shifts in diet (Baniel et al., 2021; David et al., 2014), toxin exposure (Kohl et al., 2014), and thermoregulatory demands (Khakisahneh et al., 2020; Moeller et al., 2020; Zhang et al., 2018). While data on gut microbial contributions to anticipatory plasticity remain sparse, gut microbiota may confer metabolic flexibility in light of impending environmental change, extending the range of phenotypes that can be produced in response to predictive cues by increasing energy available for hosts to draw from. Gut microbiota can enhance nutrient assimilation during periods of nutritional shortfalls through the production of microbial metabolites like short-chain fatty acids (SCFAs), which serve as *de novo* energy sources for hosts (den Besten et al., 2013). Gut microbial production of SCFAs can buffer hosts during periods of resource scarcity (Mallott et al., 2022), promoting organismal adaptation to extreme environments (Zhu et al., 2024). In birds, the metabolic demands of migration may be compensated for, at least in part, by preparatory changes in gut microbiota that enhance host energy harvest (Risely et al., 2018), and increased fat deposition in hibernating animals ahead of winter is regulated by functional change in the gut microbiota (Sommer et al., 2016; Xiao et al., 2019; Zhou et al., 2022). Intriguingly, microbial contributions to host metabolism may even allow hosts to compensate for some of the physiological costs of anticipatory responses, minimizing associated life-history trade-offs [e.g., by fueling catch-up growth while minimizing oxidative damage, (Dantzer et al., 2013, 2020)].

Gut microbiota may also mediate anticipatory shifts in host behavior and reproduction by interacting with other host physiological systems. Gut microbiota communicate with the host neuroendocrine system through a bidirectional “gut-brain axis”, for which evidence now exists beyond the lab in free-living and wild populations (Noguera et al., 2018; Petrullo, Ren, et al., 2022; Stothart et al., 2016). Through this axis, gut microbiota may drive anticipatory behavioral responses by sensing cues of future conditions, altering microbial production of hormones or other molecules, and eliciting behavioral or reproductive change [e.g., by increasing mating or foraging behavior ahead of changes in food and/or density, (Davidson et al., 2020; Schretter, 2020)]. Gut microbiota may also serve as a secondary detection system following primary integration of a predictive cue by the HPA axis. Indeed, gut microbiota appear to play a role in neuroendocrine integration of olfactory cues in rodents (Bienenstock et al., 2018), and microbial synthesis of hormones and other molecules can serve as olfactory cues for conspecific communication in some species (Ezenwa & Williams, 2014). Further, gut microbiota may integrate dietary cues to induce downstream epigenetic modifications that underlie anticipatory phenotypic adjustments (Gilbert, 2005; Jaenisch & Bird, 2003). Interactions between commensal gut microbiota and intestinal pathogens may cue anticipatory changes in reproductive investment [e.g., via fecundity compensation (Schwanz, 2008)], suggesting that microbial sensing of pathogens may index future mortality risk and/or conspecific density. As host interaction with symbiotic microbiota during development primes later-life immune function and pathogen resistance (Knutie et al., 2017), gut microbiota may also induce anticipatory modulation of the immune system in response to cues of the future pathogenic environment (Bäumler & Sperandio, 2016).

Finally, the origin source of the many commensal microbial communities is the parental microbiome, which is vertically transmitted to offspring during development in mammals and other taxa (Funkhouser & Bordenstein, 2013; Murphy et al., 2023). Thus, in response to predictive cues about the offspring environment, parents may calibrate their own microbiota to facilitate transmission of a customized suite of microbiota to offspring, shaping microbially-mediated developmental trajectories in anticipation of future conditions (Amato et al., 2024; Murphy et al., 2023). In support of this hypothesis, recent studies suggest first-time nonhuman primate mothers transmit more milk-digesting microbiota to offspring, maximizing offspring capacity for milk nutrient assimilation in anticipation of the lactational constraints associated with primiparity [vervet monkeys, (Petrullo, Baniel, et al., 2022); gelada monkeys, (Baniel et al., 2022)]. In oviparous taxa, however, eggshells present a barrier to vertical transmission: while they contain some maternal-origin microbiota, eggshells also contain environmental microbiota from the nest, which may swamp or impede microbially-mediated maternal effects (van Veelen et al., 2018). Moreover, although deterministic transmission may facilitate transgenerational anticipatory plasticity when the offspring environment is predictable, stochastic transmission may be an alternative bet-hedging strategy to maximize microbial variation among offspring when the offspring environment is instead unpredictable (Björk et al., 2019; Bruijning et al., 2022; Donaldson-Matasci et al., 2013). Future studies investigating contributions of the commensal microbiota to anticipatory plasticity will therefore benefit from testing alternative hypotheses of deterministic (e.g., via precise transmission) and stochastic (e.g., via imprecise transmission) strategies as a function of cue reliability.

5 ANTICIPATORY REPRODUCTION

The adjustment of one or more reproductive phenotypes in anticipation of future conditions (hereafter, anticipatory reproduction) is a major mechanism regulating population density and structure in some systems (Vekhnik, 2020). Anticipatory reproduction has been documented in a variety of taxa and can occur at any point in the period before, during, and after reproduction (**Figure 3**). It can have profound impacts beyond individual fitness: for instance, anticipatory increases in reproductive output ahead of a resource pulse can be a counter-strategy by consumers to eliminate the lag in a population's numerical response to an increase in prey (Boutin et al., 2006; Tissier et al., 2020), subverting predictions of classic population ecological models (Ostfeld & Keesing, 2000). Below we discuss some of the main types of anticipatory reproduction across taxa, and their underlying physiological mechanisms where known.

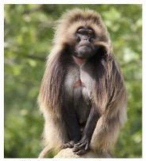
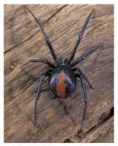
	Reproductive phenotype	Example species		
Reproductive delay	Delayed fertilization	 Guppy *(Poecilia reticulata)*		
	Embryonic diapause	 Least weasel *(Mustela nivalis)*	 *Fruit fly* *(Drosophila melanogaster)*	 Nine-banded armadillo *(Dasypus novemcinctus)*
	Embryonic resorption/litter size plasticity	 European rabbits (*Oryctolagus cuniculus)*	 *North American red squirrel (Tamiasciurus hudsonicus)*	
	Spontaneous abortion	 Norway rat *(Rattus norvegicus)*	 Gelada monkeys (*Theropithecus gelada)*	
	Pace of maturation	 Indianmeal moth (*Plodia interpunctella)*	 Australian redback spiders (*Latrodectus hasselti*)	

Figure 3. The remarkable breadth of anticipatory reproduction. Anticipatory shifts in reproductive phenotype spans a wide array of taxa, manifested through various reproductive strategies and highlighting the adaptive mechanisms that enable species to successfully navigate by optimizing functional traits like reproductive timing and litter sizes. This broad range of taxa–from insects to non-human primates–underscores the evolutionary significance of anticipatory reproductive mechanisms in fluctuating environments.

5.1 Reproductive delay

Reproductive delays can occur between mating and fertilization (delayed fertilization), fertilization and implantation (embryonic diapause), and during embryonic development following implantation. Because similar underlying mechanisms are presumed to regulate delays at all three stages, many organisms exhibit capacity for anticipatory reproductive delay at more than one stage. Some taxa, like bats, can exhibit delays at all three stages (Burns, 1981). Genetic mechanisms underlying arrested reproductive delays include epigenetic changes (e.g., small RNAs, histone modifications), circadian clock shifts, and signaling pathways of cell cycle arrest (Hand et al., 2016). Changes in the function of the HPG axis (including changes in the synthesis of estrogen, progesterone, and prolactin) are also thought to play a role in reproductive delays (Krishna & Bhatnagar, 2011). The stage at which reproductive delays occur may result from constraints within these underlying mechanisms of arrested development, and/or differences in the timing of cue perception.

5.1.1 Delayed fertilization

Delayed fertilization is often present in species in which sperm is stored in the female reproductive tract following copulation (Wimsatt, 1975). In bats, delayed fertilization is thought to be an anticipatory response to seasonal change ahead of hibernation, though not all bats that exhibit delayed fertilization hibernate (Racey & Entwistle, 2000). The ability of females to delay fertilization and maximize reproductive success appears to also elicit anticipatory counter-strategies in males (Orr & Zuk, 2013). In guppies, prolonged sperm storage facilitates adaptive timing of female reproduction, but increases sperm competition. Males respond to expected rates of competition through sperm-priming in which the final stages of sperm maturation are accelerated (Cardozo et al., 2020; Cattelan et al., 2018). Similarly, male bats in species with delayed fertilization typically grow larger testes than those in species without this type of delay (Orr & Zuk, 2013).

5.1.2 Embryonic diapause

Previously synonymous with delayed implantation, embryonic diapause is a distinct type of reproductive delay characterized by a period of suspended development at the blastocyst stage prior to implantation that can occur in insects, fish, mammals, and other taxa (Hand et al., 2016; Renfree & Fenelon, 2017). Following embryonic diapause, implantation can be immediate or delayed (Renfree & Fenelon, 2017). Diapausing mammals typically inhabit seasonal environments where day lengths, precipitation, and ambient temperatures are unstable, and embryonic diapause offers an opportunity for females to adaptively pause offspring development until conditions become more favorable (Sandell, 1990). For instance, some weasels and badgers can reproduce as early as 3-5 months of age but not give birth until the following year (Wright, 1942; Yamaguchi et al., 2006). In an extreme example, solitary American black bears (*Ursus americanus*) can optimize reproductive fitness through repeated conceptions with different paternities at multiple developmental stages (e.g., superfetation), which are then diapaused and resumed together ahead of optimal conditions (Himelright et al., 2014). However, some taxa exhibit embryonic diapause even where conditions are largely stable [e.g., in the tropics, (Wimsatt, 1975)]. In some cases, predictive cues inducing embryonic diapause have been identified but the underlying physiological mechanisms remain unknown: roe deer (*Capreolus capreolus*) use photoperiod changes to adaptively pause embryonic development ahead of winter without any change in HPG axis function (Aitken, 1974).

5.2 Reproductive output

The resorption of embryos in polytocous mammals is a flexible anticipatory strategy to adjust reproduction at one of its earliest stages, and can be partial (some embryos resorbed), or less often, complete (entire litters resorbed). In European rabbits (*Oryctolagus cuniculus*), up to 60% of litters can be resorbed depending on the timing and onset of the breeding season (Brambell, 1944), and in European brown hares (*Lepus europaeus)* and swamp rabbits (*Sylvilagus aquaticus)*, resorption occurs regularly (Conaway et al., 1960; Schroeder et al., 2011). Similar effects have been found in house mice (*Mus musculus)*, in which females can adjust sex-ratios through embryonic resorption (Krackow, 1992). In montane voles *(Microtus montaus)*, dietary and photoperiodic cues interact to regulate resorption rates: resorption rates were lower (and thus litter sizes larger) in response to experimental increases in sprouted wheat (Pinter & Negus, 1965), which is high in both fiber and phytohormones that may interact with rodent reproductive physiology (Labov, 1977). These findings echo recent work in livestock pigs in which litter sizes can be experimentally increased by modulating the gut microbiota with a high fiber diet (Che et al., 2011; Veum et al., 2009), pointing to a potential role for commensal microbiota in regulating resorption rates (and ultimately, litter sizes) in polytocous mammals. In some cases, predictive cues related to future food scarcity can trigger complete embryonic resorption. In the edible dormouse (*Glis glis)* that inhabits a resource pulse ecosystem, complete resorption occurs across all reproductively active females in anticipation of food-poor years (Vekhnik, 2019). Captivity can also increase rates of embryonic resorption, suggesting underlying mechanisms related to the physiological stress response: while American mink (*Negolae vison*) can strategically monopolize paternity through flexible embryonic resorption in the wild; in captivity, nearly half of all embryos are consistently resorbed (Hansson, 1947).

In taxa with fast generation times and relatively low costs of reproduction, reproductive output can be flexibly adjusted in response to predictive cues of both coarse- and fine-grained environmental change. In mammals, however, reproduction–especially lactation–is long and energetically costly (Speakman, 2008). Yet anticipatory reproduction continues to be documented in a variety of mammals, especially in resource pulse ecosystems [e.g., (North American and Eurasian red squirrels, (Boutin et al., 2006); yellow-necked mice, eastern chipmunks (Tissier et al., 2020), white-footed mice (Marcello et al., 2008), edible dormice (Fidler et al., 2008)]. In these ecosystems, many herbivores like rodents and ungulates rely heavily on pulsed seed, which comprise the majority of their diets (Bogdziewicz et al., 2016). As a result, granivorous rodents like edible dormice (*Glis glis*) and eastern chipmunks (*Tamias striatus*) typically only reproduce during mast years and remain inactive in years when this phenomenon does not occur (Fidler et al., 2008; Tissier et al., 2020). Among ungulates, wild boar (*Sus scrofa*) exhibit anticipatory reproduction depending on oak (*Quercus spec.*) masting by adjusting estrus timing depending on a future oak mast, facilitating earlier or delayed mating depending on future resource availability (Cachelou et al., 2022).

The key challenge for consumer populations inhabiting resource pulse ecosystems is how to maximize fitness in a rapidly changing environment. Some animals migrate (Kitchell et al., 1999), while others use scatter- or larder hoarding to cope with the instability generated by resource pulse cycles (Larsen et al., 1997; Zwolak et al., 2021). Increased reproductive output in anticipation of a mast event serves as a potential counter-strategy by consumers to circumvent the lag in their numerical response to a pulse in food by ensuring that juveniles receive an optimal food supply when their needs are greatest, promoting growth and survival. Presently, the underlying mechanisms that mediate anticipatory increases in reproductive output in resource pulse ecosystems remains largely unknown. Behavioral mechanisms like habitat selection do not appear to play a role (Dri et al., 2022). To begin to build a framework for understanding the mechanistic underpinnings of anticipatory reproductive rate increases in mammals, we can synthesize across what we know of reproductive rate adjustments in other taxa **(BOX 2).**

BOX 2. A case study in Yukon red squirrels. Female North American red squirrels (Tamiasciurus hudsonicus) in the southwest Yukon, Canada, exhibit anticipatory reproduction ahead of a resource pulse at multiple levels. In the spring and summer months, before a 3-7 year boom in their primary food source–masting white spruce (*Picea glauca*)–females reproduce earlier, increase in the number of matings, have larger litters, and successfully recruit more offspring into the breeding population (Boutin et al., 2006; McAdam et al., 2019). In some cases, females successfully wean two litters (Boutin et al., 2006; Petrullo et al., 2023). While the ultimate mechanisms driving this response include increased maternal reproductive success and higher lifetime fitness (Boutin et al., 2006; McAdam et al., 2019; Petrullo et al., 2023), to date, the proximate mechanisms that facilitate increased reproductive output remain unknown. Enhanced maternal access to food is a plausible explanation (White, 2007, 2013), but no evidence for this exists in red squirrels: models suggest that additional food is not necessary for increased reproductive output (Boutin et al., 2013), and food supplementation and larger food hoards do not increase litter sizes (Larsen et al., 1997; Petrullo et al., 2023). Alternatively, dietary shifts that prioritize certain nutrients like amino acids, which are crucial for mammalian reproduction, may fuel anticipatory plasticity (White, 2007). These nutrients could be found in other non-pulsed dietary items available during mast years. For instance, eastern chipmunks (*Tamias striatus*) increase reproductive output simultaneously with increased consumption of red maple ahead of a pulse in their primary food source [beech seed, (Tissier et al., 2020)]. This suggests that diet-switching may cue anticipatory reproduction in this population or perhaps reflect a closely related mechanism.

However, there is no evidence of diet-switching in Yukon red squirrels in mast years. Instead, squirrels may anticipate spruce mast events through exposure to springtime chemical cues that reliably predict food availability in the coming fall. Specifically, the consumption of immature sexual structures (e.g., the buds of white spruce), which emerge during the breeding season, may alert consumers to an upcoming mast event via two distinct but not mutually exclusive pathways (Descamps et al., 2008; Elliott, 1978). First, immature structures like buds contain VOCs and other substances like phytohormones (Simons & Grinwich, 1989), which can influence the reproductive physiology of consumers (Berger et al., 1981; Labov, 1977). Buds may differ in phytohormonal composition and/or concentration in resource pulse years such that their consumption in the months preceding a pulse induce anticipatory reproduction in a dose-dependent manner. Second, spruce buds may contain different macronutrient profiles compared to mature seed. Indeed, bud consumption induces a distinct microbial signature in the red squirrel gut microbiome that includes increases in taxa producing SCFAs [e.g., *Oscillospira*, (Ren et al., 2017)]. These shifts mirror those induced via increased fiber consumption, which in turn increases litter sizes in livestock (Veum et al., 2009). If bud consumption increases in mast years, nutritional and/or chemical cues may therefore trigger anticipatory reproduction by way of gut microbial reorganization. Such mechanisms may extend beyond this system: for instance, chipmunks and boar gather most of their food from the forest floor, limiting their access to immature seeds in the canopy. However, they may still pick up chemical and/or nutritional cues of an impending beech mast by consuming springtime beech or oak flowers (Berger et al., 1981; Tissier et al., 2020). Together, these hypotheses suggest possible neuroendocrine and/or microbial mechanisms linking the chemical signals emitted by masting species of trees to anticipatory reproductive change in their consumers.

5.3 Spontaneous abortion

Some animals can decrease investment in offspring–or terminate it entirely–in anticipation of a hostile future environment for offspring. When paternity is certain, infanticide can increase male fitness by accelerating a female's return to reproductive receptivity and preventing investment in offspring unrelated to a new male. But infanticide presents a problem to females due to the high biological costs of female reproduction. In some animals, females can use cues of novel males to induce spontaneous abortion and avoid future infanticide in what has been termed the "Bruce effect" (Bruce, 1960). The Bruce effect has been documented in lab mice (Bruce, 1960) and Norway rats (Marashi & Rülicke, 2012), and in wild populations of marmots [*Marmota marmota, (Hacklander, 1999)*)] and bank voles [*Myodes glareolus,* (Eccard et al., 2017)]. Evidence for this phenomenon also exists in nonhuman primates: in gelada monkeys (*Theropithecus gelada)*, 80% of gestations ended in spontaneous abortion following take-over events where an extra-group male seizes a social group, typically killing unrelated offspring (Beehner & Bergman, 2008; Roberts et al., 2012). In both examples, spontaneous abortion severs maternal investment in offspring doomed to a fate of infanticide. It also returns females to estrus sooner, facilitating earlier mating with the novel male. The proximate mechanism that underpins the Bruce effect remains largely elusive: in rodents, males may "hack" female physiology via urinary or olfactory chemical cues (e.g., male estradiol reducing female prolactin (deCatanzaro, 2023), but females may also use chemical cues of novel males to adaptively terminate reproductive investment (Zipple et al., 2019). In geladas, a comparatively smaller capacity for olfactory cue detection use may suggest a different modality, including visual cues and/or non-target effects of the physiological stress response (Roberts et al., 2012).

5.4 Adjusted pace of maturation

Adjustments to maturation rates in response to predictive cues of the future competitive and/or mating environment appear to be highly context-specific. In response to cues of high conspecific density, larvae of the male Indianmeal moth (*Plodia interpunctella)* slow reproductive maturation to facilitate the production of larger testes and more sperm, enhancing future competitive ability (Gage, 1997). When cues instead index a low-density environment, males mature more rapidly as they will need to spend more time locating females (Gage, 1997). During development, male Australian redback spiders (*Latrodectus hasselti*) respond to chemical cues of females by accelerating maturation (at the expense of body condition), but slow maturation (to facilitate attainment of better body condition) in response to chemical cues of rival males (Kasumovic & Andrade, 2006). Similar manipulation of rates of reproductive maturation in response to density cues have been described in yellow dung flies (Blanckenhorn et al., 2007) and web-building spiders (Neumann & Schneider, 2016).

6 OPEN QUESTIONS

6.1 Disentangling anticipatory plasticity from responsive plasticity

Because of the elongated time lag between predictive cue detection and future conditions inherent to anticipatory plasticity, distinguishing anticipatory responses can be difficult, but aided by two guiding principles. First, responsive plasticity can be adaptive (i.e., favored and/or maintained by natural selection), but does not have to be, while anticipatory plasticity is expected to always be adaptive: by matching phenotypes to future environmental conditions, anticipatory plasticity should always lead to increased fitness (Whitman & Agrawal, 2009). Measurement of direct fitness outcomes are thus central to distinguishing between anticipatory and responsive plasticity. However, given the potential for errors due to the extended time lag inherent to anticipatory plasticity, investigations should account for potential error mitigation strategies (Wiley, 2006), for instance by considering both short- and long-term fitness outcomes (Ghalambor et al., 2007; Petrullo et al., 2023). Fitness measures would ideally span the costs and gains associated with each phenotype expressed across each iteration of the environment in a factorial framework (DeWitt, 1998; Wiley, 2006). We recognize the difficulties of doing this in the field without long-term data on individual fitness across different environments; under controlled laboratory conditions, or through experimental manipulations like cross-fostering, phenotypes can be intentionally mismatched to future conditions in a factorial manner and resulting fitness outcomes quantified and compared (Storm & Lima, 2010).

Second, anticipatory plasticity is expected to evolve from responsive plasticity when cue reliability is high and when organisms possess the intrinsic mechanisms necessary to support anticipatory changes (Whitman & Agrawal 2009). Comparative studies in populations of the same species may reveal otherwise hidden anticipatory responses (Cachelou et al., 2022), and comparative biological surveys can illuminate the proximate mechanisms that mediate anticipatory plasticity (Guindre-Parker, 2018; Rubenstein et al., 2016; Vitousek et al., 2019). For instance, measuring physiological responses to predictive cues in different populations of the same species (e.g., where one inhabits a seasonal or resource pulse environment and the other does not) can offer insight into the physiological systems that govern anticipatory responses. Further, studies in species in which anticipatory plasticity is expected to be favored (e.g., because it would substantially boost fitness) but does not occur can shed light on anticipatory constraints (Sandell, 1984). Despite relying on pulses of catkins from masting trees, Siberian flying squirrels (*Pteromys volan*s) do not exhibit anticipatory reproduction in advance of a mast (Selonen & Wistbacka, 2016). Failure to foreshadow upcoming mast may suggest unreliable (or absent) predictive cues, and/or physiological constraints that prevent anticipatory modulation of reproductive output. Indeed, female flying squirrels can only increase reproductive output when body condition improves, and as capital breeders, they may be unable to use diet-switching or stored food to fuel anticipatory reproduction ahead of a mast (Selonen & Wistbacka, 2016).

Finally, integrative methodological approaches that capitalize on recent technological advances offer promise in revealing otherwise inconspicuous anticipatory responses. For instance, in suspected cases of anticipatory reproduction in resource pulse ecosystems, coupling non-invasive observations of feeding behavior with fecal DNA metabarcoding and/or metagenomics to track shifts in dietary intake and composition (Ando et al., 2020; Srivathsan et al., 2016; Taberlet et al., 2007) can rule out diet-switching hypotheses. Similar genomic approaches can be used to capture chemical or phytohormonal exposure within the gut microbiota (Chanclud & Lacombe, 2017; Iason, 2005), providing insight into predictive cue modalities. In the absence of direct fitness measures, experimental manipulation of factors driving responsive plasticity can provide support for adaptive organismal anticipation of future conditions. In papilonid butterflies (*Iphiclidies podalirius)*, experimental manipulation of current food quality, photoperiod, and temperature–immediate cues inducing responsive plasticity–failed to explain seasonally-induced differences in body size, suggesting that body size variation is instead an anticipatory response to upcoming seasonal change (Esperk et al., 2013).

6.2 Predicting the future in a changing world

Global climate change has led to more extreme and unpredictable weather events in many parts of the world (Thornton et al., 2014). As a result, climate warming may impede cue transmission and recognition (Kelley et al., 2018; Sih et al., 2011), and/or decrease cue fidelity (Bonamour et al., 2019). Increased artificial light at night can alter the reliability of photoperiodic cues (van Geffen et al., 2014), and eutrophication caused by nutrient pollution may diminish an aquatic organism's ability to perceive relevant shifts in photoperiod (Candolin, 2009). Visual cues can be obstructed by smog and urbanization in terrestrial organisms (Proppe, 2022), air pollution can inhibit detection of olfactory and chemical cues (Lürling & Scheffer, 2007; Weiss, 2022), and anthropogenic noise can interfere with an organism’s ability to detect important auditory cues (Kelley et al., 2018). These effects may shift reliance toward co-opted, multimodal, and mosaic cues, which may be more robust to climate-induced degradation of cue fidelity in affected populations (Abarca, 2019; Fuxjäger et al., 2019).

For anticipatory plasticity to evolve, moderate levels of environmental change are favored–if environmental conditions change too fast, plasticity may cause phenological mismatches (Kronholm, 2022). Already, female ground squirrels in the Arctic have begun to emerge from hibernation before males, reducing both male and female reproductive success (Chmura et al., 2023). Light and noise pollution are disrupting phenological patterns of cross-species interactions (McMahon et al., 2017), and molting–a typically adaptive anticipatory response to seasonal change–may become maladaptive if snow cover becomes reduced (Zimova et al., 2018). Agricultural and industrial chemicals containing xenoestrogens can bind to estrogen receptors, mimicking chemical cues that induce anticipatory changes in reproduction and wrongly foreshadowing future conditions (Ottinger et al., 2011). To minimize damage, populations relying on anticipatory plasticity to maximize fitness must therefore be able to detect and reject outdated or deceptive cues to avoid the fitness costs associated with phenotype-environment mismatching (McNamara et al., 2011)

Nonetheless, while anthropogenic change may reduce the reliability of cues, phenotypic plasticity may remain a faster strategy to enhance fitness in response to environmental change than genetic evolution [(Snell-Rood et al., 2018), but see (Fox et al., 2019)]. Populations with anticipatory mechanistic architecture already in place may be better able to more flexibly synchronize key life history traits like growth and reproduction to future food availability (Sun et al., 2018), facilitating adaptation to shifts in resources caused by climate change (Charmantier et al., 2008; Clement et al., 2023). Indeed, the epigenome–a potential mechanism underlying anticipatory plasticity–may speed adaptive evolution during its earliest stages (Kronholm & Collins, 2016). Additionally, moderate levels of gene flow driven by climate change may favor the evolution of anticipatory plasticity (Leimar & McNamara, 2015). Alternatively, newly unreliable cues will weaken selection for plasticity (Gavrilets & Scheiner, 1993), but can still preserve organismal fitness if they generate developmental variation among individuals that increases the likelihood of a match to a future environment (Donaldson-Matasci et al., 2013). A transition from anticipatory plasticity to bet-hedging, and/or toward integrative strategies combining the two, may thus be inevitable in populations where cue fidelity is disintegrating as a result of global change (Cohen, 1966; Donaldson-Matasci et al., 2013).

7 CONCLUDING REMARKS

Compared to responsive plasticity, anticipatory plasticity has been comparatively understudied despite its apparent ubiquity across phylogenies and ecologies, and its potential to serve as a mechanism of rapid organismal adaptation to environmental change. Here, we provide a needed overview of historic and recently documented cases of anticipatory plasticity, while at the same time identifying commonalities and integrating across taxa to outline potential candidate mechanisms that may underlie anticipatory plasticity. A better understanding of the commonalities between taxa that exhibit anticipatory plasticity can help to pinpoint the ecological substrates, and underlying sensory and physiological mechanisms that facilitate anticipatory responses. Consideration of populations in which anticipatory plasticity is expected to be favored but is not observed may shed light on the mechanistic constraints associated with predicting future conditions and mounting adaptive responses in anticipation of those conditions. Advances in our understanding of the mechanistic architecture that facilitates anticipatory plasticity are likely to come from highly integrative, ecophysiological studies that leverage classic physiological tools and ‘omics approaches to combine experimental frameworks with field-based studies of wild animals in their natural environments (Aubin-Horth & Renn, 2009). Given the scope at which HIREC continues to impact organisms and their broader ecosystems, a better understanding of how anticipatory plasticity may help–or hurt–how populations respond to global climate change remains a priority in the fields of functional ecology and organismal biology.

AUTHOR CONTRIBUTIONS

This study was conceived by Lauren Petrullo and Ben Dantzer. All authors (LP, BD, NJM, CT) contributed to the writing and editing of this manuscript and approved the final version.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interests to disclose.

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